Behavioral Physiology of Four Crab Species in Low Salinity

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Abstract. Reports focusing on the behavioral responses of crabs to exposure to low salinity have involved choice chamber experiments or quantification of changes in activity. In addition to describing changes in locomotor activity in four species of crabs of differing osmoregulatory ability, the present study describes six behaviors: increased movement of the mouthparts, cleaning of the mouthparts with the chelae, cleaning of the antennae and antennules with the maxillipeds, flicking of the antennae, retraction of the antennules, and extension of the abdomen. *Callinectes sapidus* and *Carcinus maenas* are classed as efficient osmoregulators, and in general, showed an increase in these behaviors with decreasing salinity. *Cancer magister*, a weak regulator, and *Libinia emarginata*, an osmoconformer, exhibited these behaviors to a lesser degree and became inactive in the lower salinities, tending to adopt an isolation-type response. The differences in behaviors between the species correlated closely with previously reported changes in cardiovascular function and hemolymph flow. These overt reactions are discussed in relation to the osmoregulatory physiology and ecology of each crab species.

Introduction

The osmoregulatory physiology of a number of crustacean species has been studied extensively during the past four decades (see Mantel and Farmer, 1983; Pequeux, 1995, for references). There are few reports on behavioral reactions to salinity variation, and these have involved either salinity choice experiments or quantification of locomotor activity.

The anomuran crab *Porcellana platycheles* displays dis-criminatory behavior in low salinity, but only outside its limits of physiological tolerance. In choice chamber experiments, this species shows rapid avoidance of salinities below 40% seawater (SW), but cannot distinguish between pairs of salinities above 40% SW (Davenport, 1972; Davenport and Wankowski, 1973). The amphipod *Corophium volutator* has a preference for salinities in the range of 10–30 ppt (30–90% SW), but only discriminates between pairs of salinities outside this range (McLusky, 1970). Comparable behavioral reactions are reported for *Marinogammarus marinus*, which has a preferred salinity range of 80%–100% SW, although it is able to survive in more dilute concentrations (Bettison and Davenport, 1976). *Carcinus maenas*, the green shore crab, increases its locomotor activity in low salinity, a behavior defined as halokinesis (Taylor and Naylor, 1977; Thomas *et al.*, 1981; Bolt and Naylor, 1985; Ameyaw-Akumfi and Naylor, 1987). Its preferred salinity range, as determined by choice chamber experiments, is 27–41 ppt (82–125% SW; Thomas *et al.*, 1981) or 17–40 ppt (51–121% SW; Ameyaw-Akumfi and Naylor, 1987), and it is able to discriminate between salinities separated by a difference as little as 0.5 ppt (McGaw, 1991). In addition, salinity choice behavior in this species is affected by the coloration of the individual and by prior acclimation salinity (McGaw and Naylor, 1992a), as well as by the availability of shelter (McGaw and Naylor, 1992b). Low salinity is also known to re-entrain and modulate the endogenous tidal locomotor rhythm in this species (Bolt and Naylor, 1985; McGaw and Naylor, 1992c).

A number of other species can control the osmotic pressure of body fluids by behavioral selection of different salinities. The coconut crab *Birgus latro* (Gross, 1995), the lined shore crab *Pachygrapsus crassipes* (Gross, 1957), and the hermit crab *Pagurus bernhardus* (Davenport *et al.*, 1980) all show modulation of behavior in response to

changes in the concentration of their body fluids. In con-
trast, the mud crab *Scylla serrata,* which is able to survive
in salinities from 2 ppt to 42 ppt (3–127% SW), shows no
discriminatory behavior between salinities in this range
(Davenport and Wong, 1987).

These behaviors ensure that the crab either escapes from
unfavorable conditions or moves to a compatible salinity
range. In either case, short-term changes in the behavior will
ultimately prevent the crab from expending energy during
longer term alterations in physiology associated with regu-
lation of the internal body fluid concentrations. Behavioral
reactions, therefore, appear to be closely related to the
physiological ability of an individual to osmoregulate.

In this paper, we describe several behaviors exhibited in
response to low salinity by four crab species of varying osmo-
regulatory abilities. The blue crab *Callinectes sapidus* is a very
efficient osmoregulator (Tan and Van Engel, 1966; Lynch *et
al.,* 1973) and can live in a range of salinities from hypersaline
lagoons to fresh water (Hedgpeth, 1967; Mangum and
Amende, 1972). Male crabs are more efficient osmoregulators
and extend further into estuaries than female or juvenile crabs
(Haefner and Schuster, 1964; Hines *et al.,* 1987). The green
shore crab *Carcinus maenas* is classed as an efficient hyper-
osmoregulator (Rankin and Davenport, 1981); it is able to
tolerate exposure to salinities as low as 5 ppt (Broekhuysen,
1936), and can even withstand short-term exposure to fresh
water (McGaw and Naylor, 1992c). The salinity tolerance of
this species is related to the coloration of the individual, which
is indicative of intermolt duration (McGaw *et al.,* 1992). Red-
colored individuals are poorer osmoregulators than green ones
(Reid *et al.,* 1989; Rasmussen and Bjerregaard, 1995) and are
absent from estuaries (McGaw and Naylor, 1992c). The
Dungeness crab *Cancer magister* is a large and commercially
important species on the west coast of North America. It lives
in sandy and muddy bays, and although it occurs in estuaries,
it is classed as a weak osmoregulator (Jones, 1941; Engelhardt
and Dehnel, 1973; Hunter and Rudy, 1975) and cannot survive
in salinities below 12 ppt (36% SW; Cleaver, 1957). The
spider crab *Libinia emarginata* is found in rocky and muddy
bays on the eastern seaboard of North America. It is classed as
an osmoconformer and can survive exposure to 40% SW if
acclimated slowly (Gilles, 1970), although the lower range of
tolerance is nearer 75%–80% SW (Cornell, 1980).

The aim of the present study was to determine whether
crab behaviors vary with salinity and time and to compare
the responses of the four species. In addition, possible
explanations for these overt reactions are discussed in rela-
tion to the physiology and ecology of each species.

Materials and Methods

Adult male crabs (intermolt stage) of each species were
maintained separately, in a recirculating artificial seawa-
ter system (Instant Ocean) at 1000–1050 mOsm (consid-
ered as 100% seawater, salinity = 33 ppt), and fed fish
twice weekly. Blue crabs (*Callinectes sapidus*) of 12–16
cm carapace width (CW) were obtained from Gulf Spec-
imen Marine Labs, Panacea, Florida, and kept at a tem-
perature of 18°–20°C. Green shore crabs (*Carcinus mae-
nas*), 4–7 cm CW (green color only), and spider crabs
(*Libinia emarginata*), 2–4 cm CW, were purchased from
the Marine Biological Laboratory, Woods Hole, Massa-
chusetts, and maintained at a temperature of 13°–15°C.
Dungeness crabs (*Cancer magister*), 16–20 cm CW,
were purchased from a local fish market and held at
11°–13°C.

The osmoregulatory ability of the crabs was determined
by acclimating eight crabs of each species to seawater
concentrations of 100%, 75%, 50%, and 25%. Acclimation
times were 24 h, with one exception: in 25% SW the
acclimation time for *Libinia emarginata* was 10 h due to
high mortality. Blood samples were taken by withdrawing a
small amount of hemolymph from the arthrodial membranes
between the walking legs. Osmolality was measured on a
vapor pressure osmometer (Westcor Inc 5100B).

Behavioral experiments were carried out in 10-gallon
aquaria with filtered aerated seawater and a layer of
gravel in the bottom. Temperatures were similar to those
in the holding tanks, and the salinity was changed by
adding a known volume of distilled water (of the same
temperature), over a 15-minute period. The behavior of
the crabs was observed for a total of 3 h. Seven separate
behaviors were observed, and these occurred to varying
degrees, depending on the salinity and species of crab.
(1) Locomotor activity: This was the only behavior that
has been described previously in relation to low salinity.
In the present study, locomotor activity was quantified
each time the crab changed location horizontally, or
vertically as it attempted to escape the aquarium. (2)
Movement of mouth parts: The third maxillipeds were
opened and closed in a side-to-side motion, which was
counted as one event. At the same time, the palps of the
maxillipeds were moved independently, and there was
rapid flicking of all the exopodites of the mouth parts. (3)
Cleaning of mouth parts: The 3rd maxillipeds and exopo-
dites of the mouth parts were scraped by the chelae;
usually one chela at a time was used. (4) Cleaning of
antennae/antennules: Both the antennae and antennules
were cleaned; they were folded down towards the max-
illipeds and the palps were scraped along the length a
number of times. (5) Flicking of antennae: The antennae
were flicked up and down, independently of each other;
each separate movement was counted as an event. (6)
Percentage time of antennule retraction: The antennules
made continuous rapid flicking movements while ex-
tended, but for periods of time they would be folded
backwards into a depression in the carapace; the approx-

imate percentage of time the antennules were retracted was recorded. (7) Percentage time of abdomen extension: This behavior was usually observed when the crab raised itself up on its legs. Initially, the last abdominal segment was opened and closed; subsequently, the entire abdomen was opened, exposing the hindgut and rectum. The crab would then either keep the abdomen open, or open and close it in a slow and regular motion.

These behaviors were recorded for 1 min at set time intervals in constant light, over a 3-h period. This time period was chosen because choice chamber experiments have shown that salinity choice is usually completed within 2–3h (Thomas *et al.*, 1981; Ameyaw-Akumfi and Naylor, 1987). A total of 16 crabs of each species were monitored in separate experiments in 100%, 75%, 50%, and 25% seawater.

Similar *P* values were obtained with Friedman's nonparametric ANOVA and with standard repeated measures ANOVA on normalized data. The latter test was therefore used because it allowed significant interactions to be followed up with Student-Newman-Keuls tests on pairwise comparisons of each salinity.

Results

There was a difference in osmoregulatory ability between each of the four crab species (Fig. 1). *Callinectes sapidus* was the most efficient osmoregulator, and even in 100% seawater its hemolymph osmolality was higher than that of the other species. The hemolymph osmolality of each species was similar in 75% seawater, but in 50% and 25% SW, there was a gradation. *Callinectes sapidus* had the highest mean hemolymph osmolality of 690 mOsm. *Libinia emarginata* was an osmoconformer with a hemolymph osmolality close to that of the ambient seawater. The osmoregulatory ability of *Carcinus maenas* and *Cancer magister* lay in between these two extremes, with the former being the more efficient osmoregulator.

Locomotor activity increased in all four species as the salinity decreased (Fig. 2). In *Callinectes sapidus*, there was a large variation between individual crabs. Although there was a strong trend towards greater activity in low salinity, at the end of the 3 h-test period (not shown) there was no statistically significant difference in activity levels ($F = 1.21$, $P > 0.05$; Table I). Locomotor activity was more
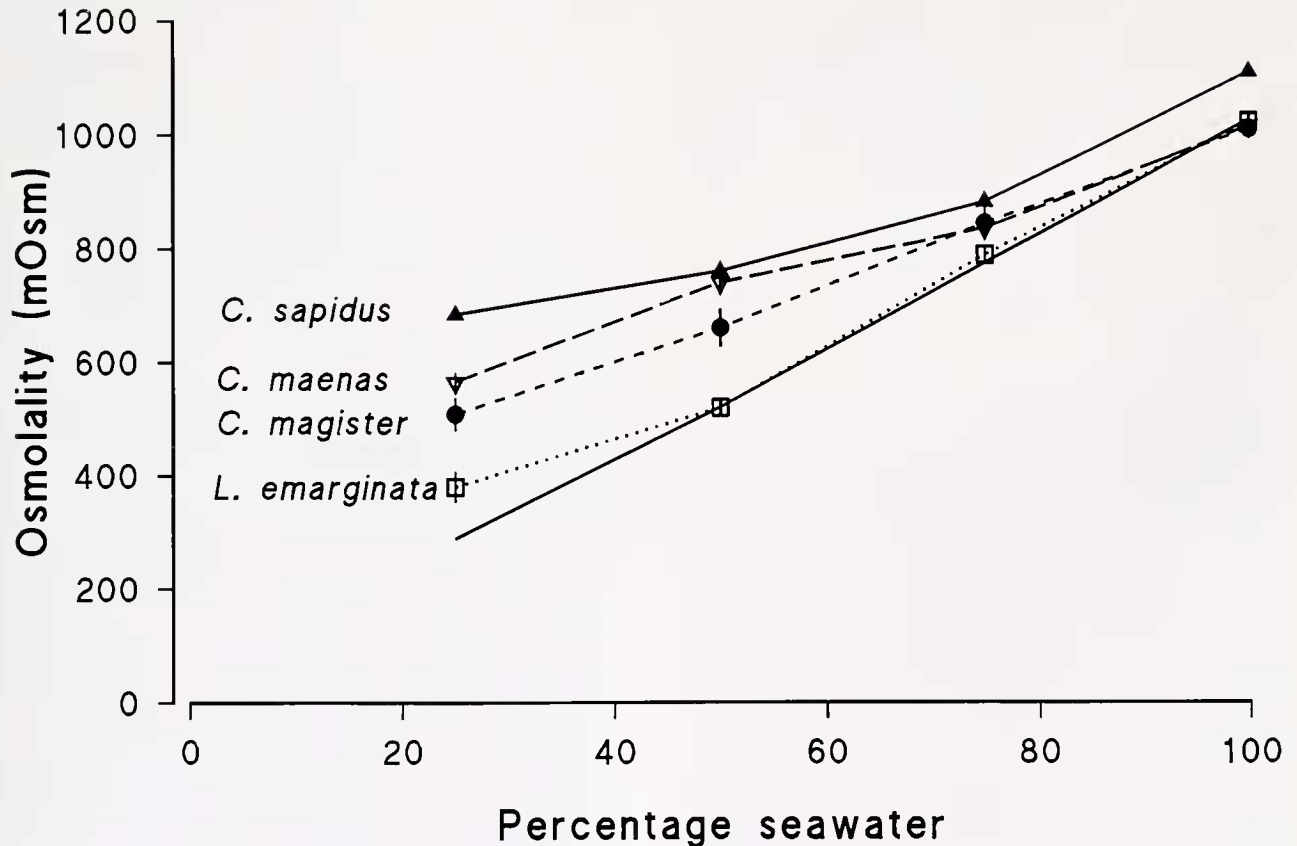

Figure 1. Hemolymph osmolality (mean ± SEM) of 8 male *Callinectes sapidus, Carcinus maenas, Cancer magister,* and *Libinia emarginata* in seawater concentrations of 100%–25%, shown in relation to iso-osmotic line for each seawater concentration.
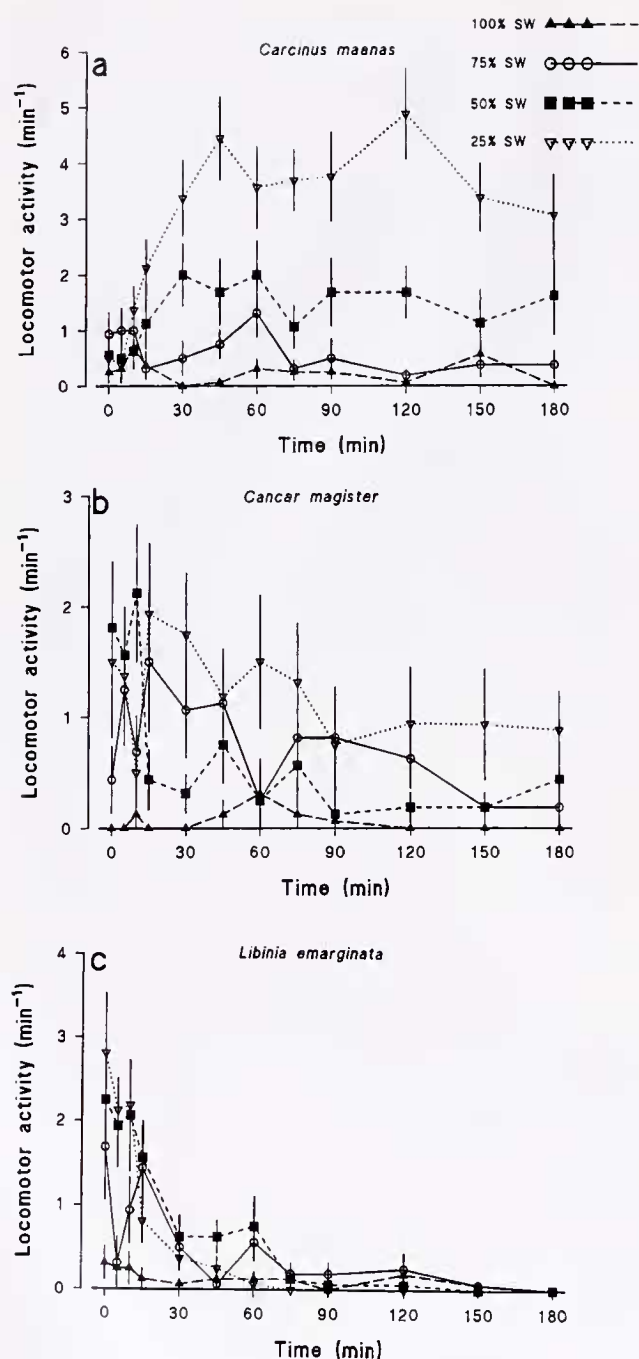
Figure 2. Locomotor activity of 16 crabs (mean ± SEM) during 3-h exposure to seawater concentrations of 100%, 75%, 50%, and 25% seawater; (a) *Carcinus maenas*, (b) *Cancer magister*, and (c) *Libinia emarginata*.

the experiment. Both *Cancer magister* (Fig 2b) and *Libinia emarginata* (Fig. 2c) showed an immediate and significant increase in activity as the salinity was lowered ($F = 7.46$ and 7.60, $P < 0.000$). However, the pattern was somewhat different than in *Callinectes sapidus* and *Carcinus maenas*. The activity levels of *Cancer magister* declined during the first hour of low-salinity exposure, and *Libinia emarginata* was largely inactive after 45 min. Individuals of both species buried themselves in the gravel and moved infrequently thereafter.

Each species also responded to a decrease in salinity with an increase in frequency of mouthpart movements; each set of mouthpart movements (3–8 movements per set) was associated with a ventilatory reversal (not shown). In *Callinectes sapidus*, there was a clear increase in mouthpart movements as the seawater was lowered to 25% (Fig. 3a; $F = 23.29$, $P < 0.000$). In 100% seawater this species only occasionally opened its mouthparts, but in 50% and 25% seawater the frequency of mouthpart movements was elevated for the 3-h experimental period. *Carcinus maenas* exhibited a similar behavior pattern, with increasing mouthpart movements in the lower salinities (Fig. 3b; $F = 20.11$, $P < 0.000$). In 50% and 25% SW there was a significant increase in frequency of mouthpart movements compared to levels in 100% and 75% SW (Table 1); this was maintained for the duration of the experiment. In *Cancer magister* (Fig. 3c), there was a significant increase in mouthpart movements in all salinities below 100% seawater ($F = 4.55$, $P < 0.01$); but unlike *Callinectes sapidus* and *Carcinus maenas*, *Cancer magister* did not maintain the increase. The number of mouthpart movements quickly declined, reaching levels equivalent to those in 100% SW after 30–45 min. In *Libinia emarginata* (Fig. 3d), a similar trend was observed, with a short-term increase in frequency of mouthpart movements in 25% SW ($F = 3.25$, $P < 0.05$), which decreased within an hour to levels comparable to those in 100% SW. The overall trend was a decrease in the frequency of mouthpart movements with decreasing osmoregulatory ability of each crab species (Fig. 1, Fig. 3a–d).

The crabs used their chelae to scrape the third maxillipeds and exopodites of the mouthparts; this behavior was only observed during the first hour of low-salinity exposure. Both *Callinectes sapidus* (Fig. 4a) and *Carcinus maenas* (Fig. 4b) cleaned their mouthparts only in the lowest salinity tested (25% SW; $F = 12.26$ and 11.65, $P < 0.000$). In *Callinectes sapidus* this behavior stopped after 90 min (Fig. 4a), whereas in *Carcinus maenas* it was not observed after 45 min (Fig. 4b). Only a small percentage of *Cancer magister* individuals actually cleaned their mouthparts (Fig. 4c), and the increase in this behavior was significant only in 50% seawater ($F = 4.6$, $P < 0.01$; Table 1). *Libinia emarginata* (Fig. 4d) showed a significant increase in mouthpart cleaning in 50% and 25% SW ($F = 13.37$, $P < 0.000$; Table

pronounced in *Carcinus maenas*. There was a significant increase after 15–30 min in 50% and 25% seawater (Fig. 2a; $F = 22.45$, $P < 0.000$), and activity remained elevated above levels in 100% and 75% seawater, for the duration of

Table 1

Student-Newman-Keuls pairwise tests for significant differences in behavior of each crab species, between each of the four salinities tested

	Percentage Seawater Comparison					
	100 vs 75	100 vs 50	100 vs 25	75 vs 50	75 vs 25	50 vs 25
Callinectes sapidus						
Locomotor activity	NS	NS	NS	NS	NS	NS
Mouthpart movement	NS	*	*	*	*	*
Mouthpart cleaning	NS	NS	*	NS	*	*
Antennae cleaning	NS	*	*	NS	*	NS
Antennae flicking	NS	NS	NS	NS	NS	NS
Antennule retraction	*	*	*	NS	NS	NS
Abdomen extension	NS	NS	NS	NS	NS	NS
Carcinus maenas						
Locomotor activity	NS	*	*	NS	*	*
Mouthpart movement	NS	*	*	*	*	NS
Mouthpart cleaning	NS	NS	*	NS	*	*
Antennae cleaning	*	*	*	*	*	NS
Antennae flicking	*	*	*	NS	NS	NS
Antennule retraction	NS	*	NS	NS	NS	NS
Abdomen extension	NS	NS	*	NS	*	*
Cancer magister						
Locomotor activity	*	*	*	NS	NS	NS
Mouthpart movement	*	*	*	NS	NS	NS
Mouthpart cleaning	NS	*	NS	NS	NS	*
Antennae cleaning	NS	NS	NS	NS	NS	NS
Antennae flicking	NS	NS	*	NS	NS	NS
Antennule retraction	*	*	*	*	*	*
Abdomen extension	NS	NS	*	NS	*	*
Libinia emarginata						
Locomotor activity	*	*	*	NS	NS	NS
Mouthpart movement	NS	NS	*	NS	NS	NS
Mouthpart cleaning	NS	*	*	*	*	*
Antennae cleaning	NS	NS	NS	NS	NS	NS
Antennae flicking	NS	NS	NS	NS	NS	NS
Antennule retraction	*	*	*	NS	NS	NS
Abdomen extension	NS	NS	*	NS	*	*

NS = not significant; * = significant ($P < 0.05$).

1), and as with the other species, this behavior ceased after 45 min.

Both *Callinectes sapidus* (Fig. 5a) and *Carcinus maenas* (Fig. 5b) cleaned the antennae and antennules with the palps of the third maxillipeds, and this behavior increased with decreasing salinity ($F = 10.85$ and 11.86, $P < 0.000$). *Callinectes sapidus* showed an increase in frequency of cleaning in 50% and 25% SW, whereas *Carcinus maenas* increased antennae and antennule cleaning in 75% SW, as well as in the two lowest salinities (Table 1). Antennae or antennule cleaning essentially did not occur in *Cancer magister* or *Libinia emarginata* (not shown): only one or two individuals of each species exhibited this behavior, hence the insignificant value ($P > 0.05$).

In *Callinectes sapidus* the antennae were flicked up and down, on average, 2–3 times per minute, and this did not change with salinity (Table 1; $F = 2.35$, $P > 0.05$). There was also no significant change in antennae flicking in *Li-binia emarginata* ($F = 0.83$, $P > 0.05$), since this behavior was only observed in two individuals in 25% SW. In *Carcinus maenas* there was an increase in antennae flicking in all salinities below 100% SW ($F = 7.04$, $P < 0.000$; Table 1), which increased in frequency as the salinity decreased. In *Cancer magister*, there was a similar increase in frequency of antennae flicking; however, rates were significantly elevated only in 25% SW ($F = 3.04$, $P < 0.05$; Table 1). In each case there was a large variation in this behavior between each of the salinities.

The antennules of all the crabs were flicked rapidly while orientated in different directions, but were also retracted into the carapace for periods of time. In 100% SW each species retracted the antennae for about 5–20 s of every minute (10%–30%), but distinct differences between the species occurred in the lower salinities (Fig. 6). *Callinectes sapidus* (Fig. 6a) retracted its antennules upon initial exposure to 25% SW, but after 10 min the antennules were rarely
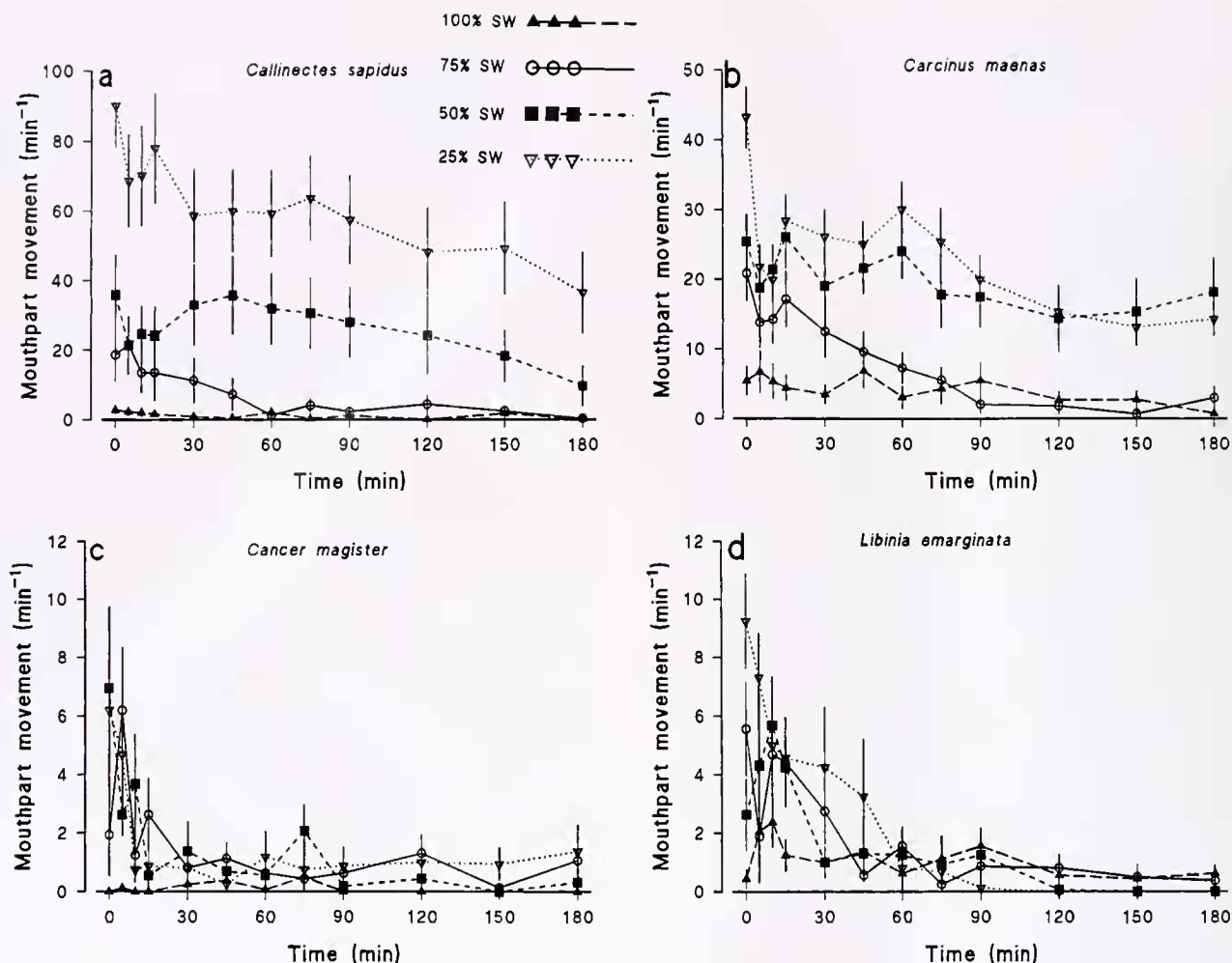
Figure 3. Mouthpart movements of 16 crabs (mean ± SEM) during 3-h exposure to seawater concentrations of 100%, 75%, 50%, and 25% seawater: (a) *Callinectes sapidus,* (b) *Carcinus maenas,* (c) *Cancer magister,* and (d) *Libinia emarginata.*

retracted; in 75% and 50% SW the antennules remained extended for the entire experimental period ($F = 24.24$, $P < 0.000$). Although the pattern was similar in *Carcinus maenas* (Fig. 6b), with the antennules exposed for longer periods in all salinities below 100%, this was statistically significant only in 50% SW ($F = 4.48$, $P < 0.01$). In *Cancer magister* and *Libinia emarginata,* the opposite response was seen: in low salinities the animals retracted the antennules. *Cancer magister* (Fig. 6c) showed a stepwise and significant increase in antennule retraction ($F = 27.32$, $P < 0.000$) in decreasing salinities, with the antennules more-or-less retracted for 100% of the time in 25% SW. *Libinia emarginata* (Fig. 6d) also retracted the antennules to a greater degree (60%–80% of the time) in all salinities below 100% SW ($F = 33.88$, $P < 0.000$), but there was no significant difference in retraction times between 75%, 50%, and 25% SW, as occurred in *Cancer magister* (Fig. 6c).

Crabs extended their abdomens in 50% and 25% SW

only, although this behavior was also observed in some animals when returned to 100% SW in the holding tanks. *Callinectes sapidus* did not extend the abdomen to any significant degree ($F = 1.77$, $P > 0.05$): only three animals were observed to extend the last segment of the abdomen in 25% SW, for short periods of time (not shown). *Carcinus maenas* extended the entire abdomen during the first hour in 25% SW and to a lesser degree in 50% SW (Fig. 7a), and this was usually accompanied by slow fanning movements of the abdomen; however, this was significantly different from control levels only in 25% SW ($F = 12.03$, $P < 0.000$). *Cancer magister* (Fig. 7b) also extended the abdomen in 50% and 25% SW, although the time course for this behavior was more erratic. Again, this behavior was only significantly different from the control in 25% SW ($F = 9.95$, $P < 0.000$). Abdomen extension increased steadily ($F = 12.35$, $P < 0.000$) in *Libinia emarginata* (Fig 7c) after 1 h exposure to 25% SW. This appeared to be a passive
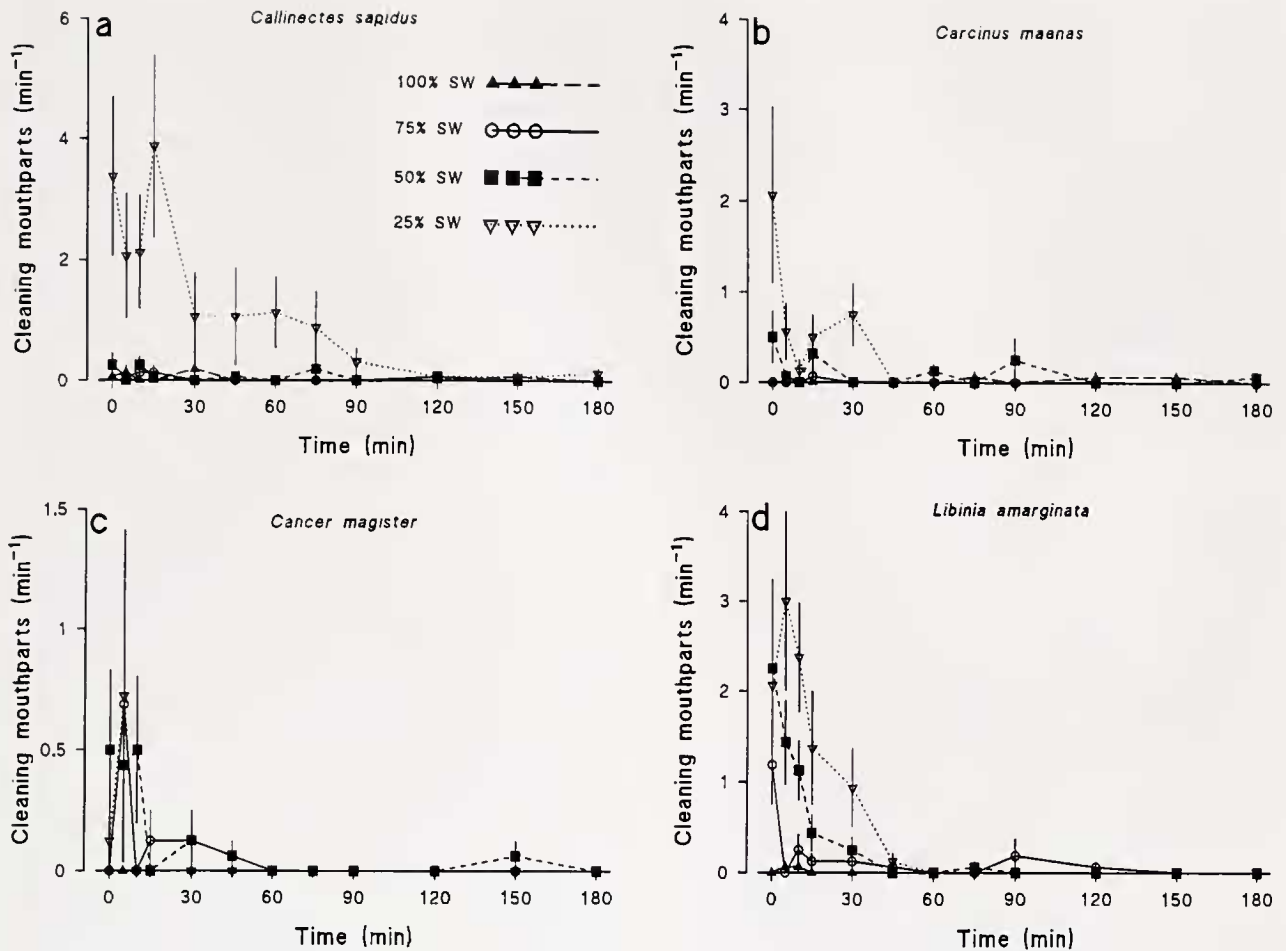
Figure 4. Cleaning of the mouthparts in 16 crabs (mean ± SEM) during 3-h exposure to 100%, 75%, 50%, and 25% seawater: (a) *Callinectes sapidus,* (b) *Carcinus maenas,* (c) *Cancer magister,* and (d) *Libinia emarginata.*

process, rather than the extension and fanning of the abdomen seen in the other species.

Discussion

Callinectes sapidus hyper-regulated its body fluids in all salinities, including 100% SW (Fig. 1); this has been reported previously (Tan and Van Engel, 1966). In all the other species, hemolymph was iso-osmotic with 100% SW. *Carcinus maenas,* which is classed as an efficient osmoregulator, had hemolymph osmolality levels (Fig. 1) similar to previous reports (Lucu *et al.,* 1973; Rankin and Davenport, 1981). All *Carcinus* used in the present study were green-colored male crabs. Red-colored individuals, which are in a prolonged intermolt (McGaw *et al.,* 1992), are poorer osmoregulators (Reid *et al.,* 1989; McGaw, 1991) and have different behavioral responses to low salinity (McGaw and Naylor, 1992a, c). *Cancer magister* is classed as a weak osmoregulator (Jones, 1941) and the levels of hemolymph

osmolality reported here (Fig. 1) agree closely with the data of Hunter and Rudy (1975). *Cancer magister* is able to survive in salinities as low as 12 ppt (36% SW; Cleaver, 1957); however, in the present study all survived short-term exposure (24 h) to 25% SW (8 ppt) (Fig. 1). *Libinia emarginata* is an osmoconformer, with ion levels closely following those of the external medium (Gilles, 1970). This was also seen in the present study (Fig. 1), except in the lowest salinity. *Libinia emarginata* can withstand dilution of the medium only to 40% SW (Gilles, 1970). Mortality was high after 12-h exposure to 25% SW, and the short acclimation time (10 h) used would not have allowed hemolymph osmolality to decline to stable levels (Fig. 1).

Most reports on the activity of crabs in low salinity pertain to *Carcinus.* Taylor and Naylor (1977) report that *Carcinus maenas* responds to a lowering of salinity with an increase in locomotor activity, defined as halokinesis. This has been confirmed by a number of other studies (Taylor *et*
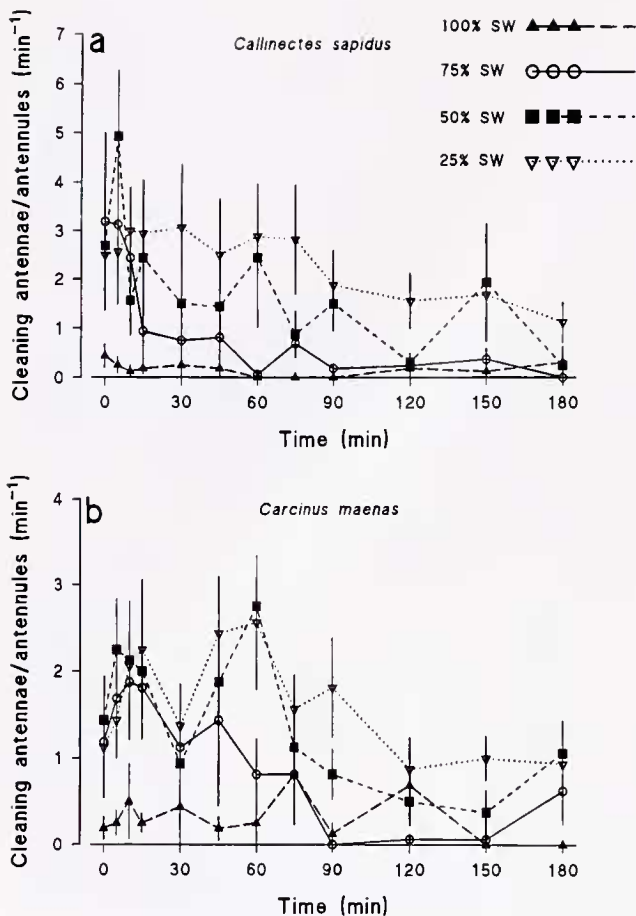
Figure 5. Antennae/antennule cleaning of 16 crabs (mean ± SEM) during 3 h in 100%, 75%, 50%, and 25% seawater: (a) *Callinectes sapidus*, (b) *Carcinus maenas*.

al., 1977; Thomas *et al.*, 1981; Bolt and Naylor, 1985; Ameyaw-Akumfi and Naylor, 1987; Warman *et al.*, 1991); such behavior enables the crab to escape deleterious salinities. In the present study, this increase in activity was not shown by all the crab species (Fig. 2b, c). Although *Callinectes sapidus* responded to a decrease in salinity with an increase in activity, this increase proved to be statistically insignificant. This species can live for extended periods in fresh water (Mangum and Amende, 1972), and therefore an escape response would be unnecessary. Likewise, the mud crab *Scylla serrata*, which can survive in 2 ppt salinity (Hill, 1979), shows no increase in activity and no preference for a particular medium (Davenport and Wong, 1987). *Carcinus maenas* showed a clear increase in locomotor activity with decreasing salinity (Fig. 2a), thus confirming the previous reports. Activity levels were noticeably higher in 25% SW, probably because this salinity approaches the lower limits of tolerance for the species (Broekhuysen, 1936). *Cancer magister* showed an increase in locomotor activity in all salinity below 100% SW, but this behavior was different than

that exhibited by *Callinectes sapidus* and *Carcinus maenas*. About half of the animals ceased activity soon after salinity reduction, remaining motionless with the eyes and antennae retracted; the majority of individuals were inactive after 60–90 min (Fig. 2b). This behavior was more pronounced in *Libinia emarginata* (Fig. 2c); these crabs were active for only 30–60 min before ceasing activity. This was not due to water loading and impairment of movement as it is in porcelain crabs (Davenport, 1972), since inactive *Cancer magister* and *Libinia emarginata* reacted aggressively and resumed activity when probed with a glass rod.

This difference in locomotor activity between the species is echoed in their cardiovascular responses to low salinity. *Callinectes sapidus* reacts to a dilution of the medium with an immediate increase in heart rate and cardiac output, which eventually leads to increased venous return through the gills (McGaw and Reiber, 1998). Likewise, *Carcinus maenas*, which also exhibits increased locomotor activity, shows an increase in heart rate (Hume and Berlind, 1976; Taylor, 1977) as well as in calculated cardiac output and gill blood flow (Spaargaren, 1974, 1982). Although *Cancer magister* increases heart rate in 50% SW, cardiac stroke volume actually decreases, leading to a substantial decrease in cardiac output and gill blood flow (McGaw and McMahon, 1996). Cornell (1993, 1974) reports a corresponding decrease in heart rate (and presumably cardiac output) of *Libinia emarginata* in low salinity. In addition, hemolymph flow to the muscles of the legs *via* the sternal artery (Pearson, 1908; McLaughlin, 1983) increases in *Callinectes sapidus* (McGaw and Reiber, 1998), possibly reflecting increased metabolic demand of the locomotory muscles (Fig. 2a). In contrast, hemolymph flow through the sternal artery of *Cancer magister* decreases (McGaw and McMahon, 1996), as does activity after 60 min (Fig. 2b). In crabs, differential hemolymph flow and changes in cardiac function are controlled by pericardial hormones (Airriess and McMahon, 1992; McGaw and McMahon, 1995, 1999; McGaw *et al.*, 1994a, 1995) and possibly by neurohormones from the X-organ complex (McGaw and McMahon, 1998). A variety of neurohormones are known to have multiple effects on the osmoregulatory physiology of crustaceans, including modulation of cardiovascular parameters (see Kamemoto, 1976; Pequeux, 1995).

There were distinct differences in movement of the mouthparts (third maxillipeds and exopodites) between each of the species (Fig. 3). Each set of maxilliped movements corresponds to a ventilatory reversal (McGaw, unpubl. data), with water being taken in through the mouth, directed backwards towards the posterior gills, and ejected through the Milne Edwards opening at the base of the legs (Arudpragasam and Naylor, 1964, 1966; Hughes *et al.*, 1969). The exact function of these reversals is not known, but they are thought to aid in clearing the gill chambers of debris as well as irrigating the posterior gills (Arudpragasam and Naylor,
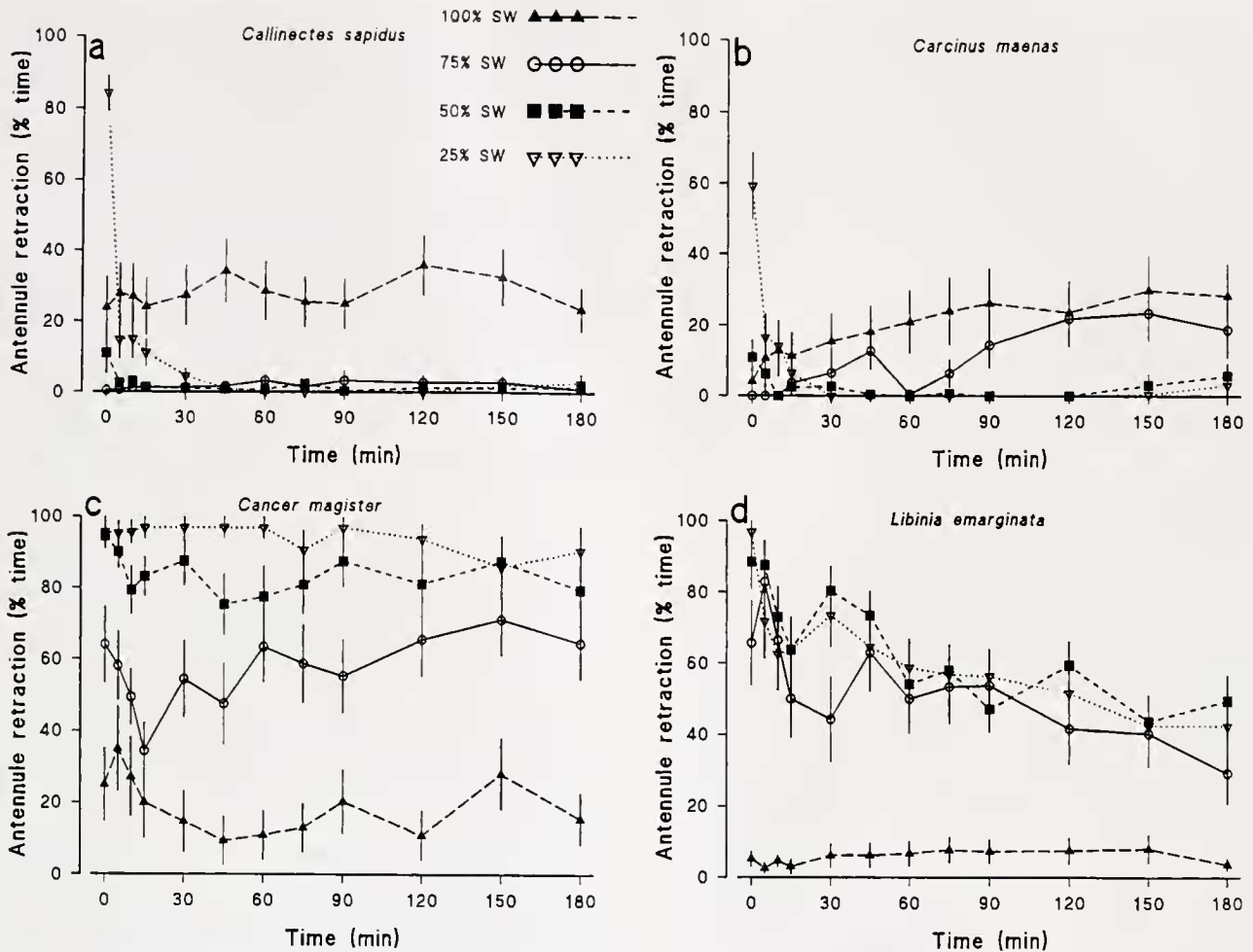
Figure 6. Percentage time of antennule retraction of 16 crabs (mean ± SEM) during 3 h in seawater concentrations ranging from 100%–25%: (a) *Callinectes sapidus*, (b) *Carcinus maenas*, (c) *Cancer magister*, and (d) *Libinia emarginata*.

1964, 1966). Evidence suggests that the posterior gills have the highest Na-K-ATPase activity (Florkin and Schoffeniels, 1969; Neufeld *et al.*, 1980; Siebers *et al.*, 1982, 1983, 1985, 1986), and therefore a ventilatory reversal would bring water into contact with the pumps of the posterior gills, enhancing active ion uptake. In support of this concept, *Callinectes sapidus*, which is the most efficient osmoregulator tested, exhibits the highest frequency of mouthpart movements (and hence ventilatory reversals; Fig. 3a), and this behavior decreases with the declining osmoregulatory ability of the species (Fig. 3), with the weak osmoregulator *Cancer magister* (Fig. 3c) and the stenohaline *Libinia emarginata* (Fig. 3d) showing substantially less ventilatory reversals than the two efficient osmoregulators (Fig. 3a, b). In addition, both *Callinectes sapidus* (Fig. 3a) and *Carcinus maenas* (Fig. 3b) showed a stepwise increase in mouthpart movements with decreasing salinity; this increase was sustained in 50% and 25% SW, for the 3-h experimental period. In both *Cancer magister* and *Libinia emarginata*

(Fig. 3c, d; Table I), mouthpart movements increased only during the first 30 min. Thereafter, the crabs kept the mouthparts sealed, isolating the branchial chamber. This sealing of the branchial chambers has been reported previously for *Cancer magister* (Sugarman *et al.*, 1980). Isolation of the branchial chambers, in conjunction with a decrease in gill blood flow *via* a reduced cardiac output (McGaw and McMahon, 1996; Cornell, 1973, 1974), would help reduce the gradient for water uptake and diffusive salt loss.

There are also differences in hemolymph flow to the muscles of the mouthparts, which are supplied by the sternal artery and branches of the anterolateral arteries (Pearson, 1908; McLaughlin, 1983). In *Callinectes sapidus*, hemolymph flow through the sternal artery and anterolateral arteries is elevated for 2–4 h in 25% SW (McGaw and Reiber, 1998), which corresponds to the period of increased mouthpart movement (Fig. 3a). In contrast, blood flow through the sternal artery and anterolateral arteries of *Cancer magister* decreases (McGaw and McMahon, 1996), and
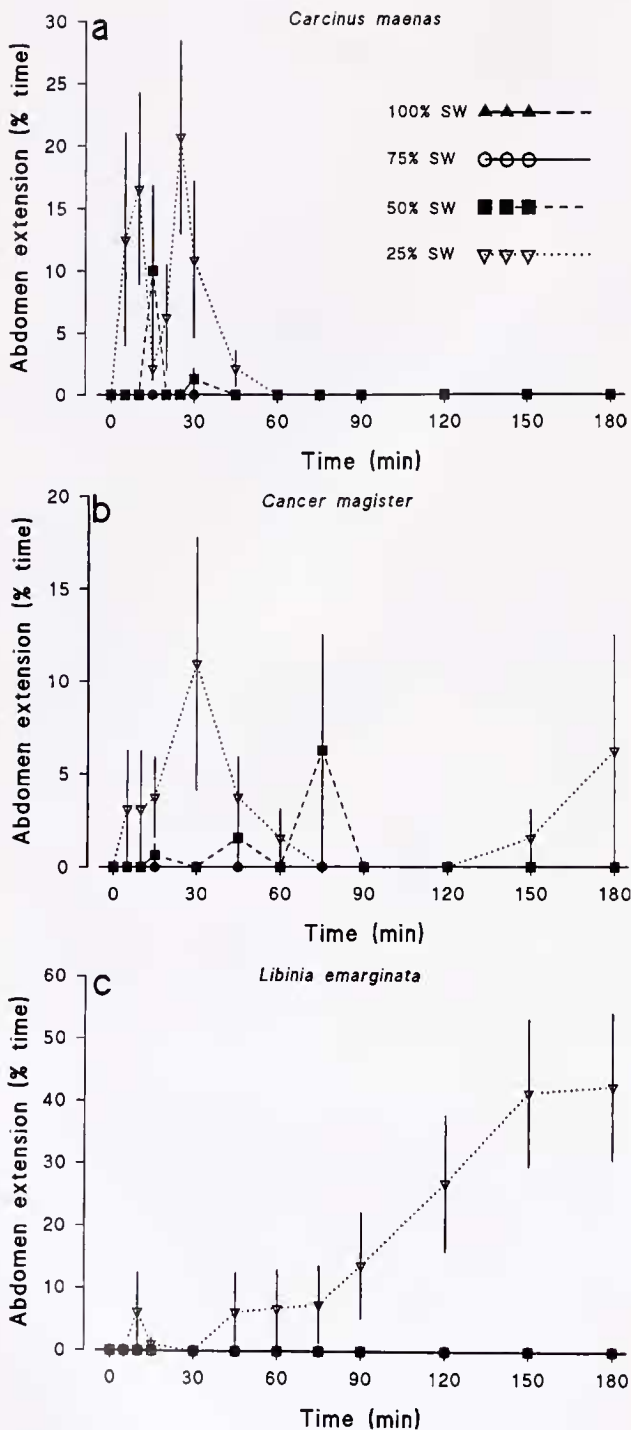
Figure 7. Mean abdomen extension (% time) of 16 crabs during a 3-h period in 100%–25% seawater concentrations: (a) *Carcinus maenas*, (b) *Cancer magister*, and (c) *Libinia emarginata*.

this parallels the rapid decrease in the number of mouthpart movements seen in this species after 15 min in low salinity (Fig. 3c).

All species of crabs cleaned their mouthparts with the

chelae (Fig. 4); this occurred only during the first hour of low-salinity exposure, and was most evident in the lowest salinity tested. The reasons for this behavior are unclear, but the short time period suggests that it could be a startle response to the initial salinity change, possibly due to irritation of the setae of the mouthparts, which have a chemosensory function (Shelton and Laverack, 1970). This behavior was evident only in 25% SW in both *Callinectes sapidus* (Fig. 4a) and *Carcinus maenas* (Fig. 4b), but became more pronounced in 50% SW in the other two species. Although *Cancer magister* (Fig. 4c) cleaned the mouthparts more often in all salinities below 100%, the frequency of this behavior was low and it was statistically significant only in 50% SW. *Libinia emarginata* (Fig. 4d) showed a significant increase (Table I) in mouthpart cleaning in both 50% and 25% SW.

Differences in hemolymph flow are again observed between the species. *Callinectes sapidus* shows an increase in hemolymph delivered to the chelae *via* the sternal artery (McGaw and Reiber, 1998), which correlates with their increased use. *Cancer magister*, in contrast, shows a reduced blood flow through the sternal artery (McGaw and McMahon, 1996). Only four individual *Cancer magister* were observed to clean their mouthparts, hence the low mean frequency (0.5 min^{-1}; Fig. 4c). This would explain why the increase in flow that occurs in *Callinectes sapidus* is not evident in *Cancer magister*.

In both the efficient osmoregulators, *Callinectes sapidus* and *Carcinus maenas* (Fig. 5a, b), there was a stepwise increase in cleaning of the antennae and antennules with decreasing salinity (Table I). This behavior was not observed in the weak osmoregulator *Cancer magister* or the stenohaline *Libinia emarginata* (Table I). Recent evidence (Gleeson *et al.*, 1996, 1997) shows that the dendrites in the olfactory sensilla of the antennules of blue crabs are osmotically ablated in low salinity. Cleaning of the antennules (Fig. 5a) may be the response to the sensory loss or irritation resulting from the osmotic destruction of the dendrites. Cleaning of the antennules ceases after a number of hours in low salinity (Fig. 5), possibly allowing for their regeneration, which takes 48–96 h (Gleeson *et al.*, 1996). Changes in hemolymph flow to the muscles of the mouthparts, *via* the sternal and anterolateral arteries, compare closely with their use. *Callinectes sapidus* shows an increase in hemolymph flow through these vessels for 2–4 h after low-salinity exposure (McGaw and Reiber, 1998), whereas *Cancer magister*, which doesn't clean the antennae with the mouthparts (Table I), has about a 50% decrease in hemolymph flow during 6 h of exposure to 50% SW (McGaw and McMahon, 1996).

In conclusion, the increase in hemolymph flow through the anterolateral and sternal arteries of *Callinectes sapidus* (McGaw and McMahon, 1998), and the concurrent decrease in the same arteries of *Cancer magister* (McGaw and Mc-

Mahon, 1996), is a result of change in blood demand, probably caused by a combination of alterations in mouthpart movement and in mouthpart and antennae/antennule cleaning, with changes in locomotor activity having a lesser effect (Figs. 2–5).

The antennae and antennules of crustaceans have been implicated as having a chemosensory role in salinity detection (Krijgsman and Krijgsman, 1954; Lagerspetz and Mattila, 1961; Van Weel and Christofferson, 1966; Davenport, 1972; Tazaki, 1975; Gleeson et al., 1996, 1997). Both the antennae and antennules were flicked up and down during the experiments. Although Callinectes sapidus flicked the antennae, there was no change in rate with salinity (Table 1). In Libinia emarginata, the antennae were small and rarely moved. There was a slight increase in antennae flicking of Cancer magister, but only in the lowest salinity. Carcinus maenas was the only species to show a significant increase in all lowered salinities (Table 1). However, with such variability within and between the species, it is hard to draw conclusions as to the role of the antennae in salinity detection; indeed, only a few papers cite the antennae as the sites of salinity reception (Lagerspetz and Mattila, 1961; Tazaki, 1975).

The percentage of time that the antennules were folded back into the carapace was recorded because flicking was too rapid to allow accurate determination of rate. Callinectes sapidus and Carcinus maenas exhibited similar behaviors (Fig. 6a, b): in 100% SW the antennules were retracted for 20%–25% of time; in the lowest salinity tested (25% SW) they were retracted during the initial salinity change-over period, but remained extended thereafter (Fig. 6a, b); in 50% and to a degree in 75% SW the antennules were rarely retracted. The opposite pattern was observed in the other two species. In 100% SW the retraction times were somewhat similar to those of Callinectes sapidus and Carcinus maenas; but in Cancer magister there was an increase in retraction with decreasing salinity, to the point that the antennules were retracted for nearly 100% of the time in 25% SW (Fig. 6c). In Libinia emarginata, too, there was an increase in retraction time in all salinities below 100% SW (Fig. 6d). Possibly these two species avoid low-salinity exposure with an isolation-type response. These results, as well as other behavioral and physiological work (Krijgsman and Krijgsman, 1954; Van Weel and Christofferson, 1966; Davenport, 1972; Sugarman et al., 1980; Gleeson et al., 1996, 1997), suggest that the antennules are more important than the antennae for salinity detection. In addition to the antennae and antennules, crabs possess hair-peg organs on many areas of the carapace, and these could be also be used for salinity detection (Schmidt, 1989).

Extension and flicking of the antennules of Callinectes sapidus is paralleled by increased hemolymph flow through the anterior aorta (McGaw and Reiber, 1998), which supplies these structures (Pearson, 1908; McLaughlin, 1983),

and by a decrease in flow in the same artery of Cancer magister (McGaw and McMahon, 1996). When Cancer magister was returned to 100% SW, the antennules were extended again and rapidly flicked from side to side, and flow through the anterior aorta also increased at this time (McGaw and McMahon, 1996).

A number of individuals of each species were observed extending the abdomen for short periods or fanning it up and down. This behavior was not statistically significant in Callinectes sapidus, since only three crabs opened the last segment of the abdomen (Table 1). Carcinus maenas (Fig. 7a) and Cancer magister (Fig. 7b) increased abdomen extension in 50% and 25% SW, although it proved to be significant only in 25% SW (Table 1). Libinia emarginata also extended the abdomen (Fig. 7c) but it wasn't considered to be the same active behavior involving fanning and retraction. It occurred later in the experiment, increased progressively, and was probably caused by swelling of the tissues due to increased water loading. Extending the abdomen brings the soft tissues of the hindgut and rectum into direct contact with the water. Crustaceans and other arthropods can use the hindgut for osmotic and ionic regulation (Heeg and Cannone, 1966; Kamemoto, 1976; Malley, 1977; Phillips et al., 1986; Audsley et al., 1992); abdomen extension could, therefore, function as an additional means of ion uptake in low salinity.

There are also interspecific changes in blood flow to the abdomen and hindgut, which is perfused by the posterior aorta (Pearson, 1908; McLaughlin, 1983). Callinectes sapidus shows no change in hemolymph flow through this artery upon salinity reduction. In contrast, an increase in flow through the posterior aorta of Cancer magister occurs during low-salinity exposure, and on return to 100% SW (McGaw and McMahon, 1996). In Cancer magister, abdomen extension occurs in low salinity and for short periods upon return to 100% SW. Increased blood flow would supply the extensor muscles of the abdomen and may also aid in ion exchange across the hindgut.

Previous work on behavioral reactions of crabs to low salinity is largely confined to efficient osmoregulators, which show active avoidance of low salinity, changes in physiology, or both. These efficient hyperosmotic regulators actively uptake ions from the environment across their gills and eliminate excess water gained by osmosis, through the production of an iso-osmotic (to the hemolymph) urine (Pequeux, 1995). The hyperosmoregulating crabs (Callinectes sapidus, Carcinus maenas) responded to a decrease in salinity with an increase in activity, which may serve as an initial escape response (Fig. 2a, b). In addition, a number of other behavioral mechanisms may enhance the ability of these species to tolerate the low-salinity exposure. An increase in mouthpart movements (Fig. 3a, b) was correlated with ventilatory reversals that may increase the efficiency of ion exchange between the water and the posterior gills.

Chemoreceptors on the antennae and antennules were moved through the water during low-salinity exposure (cleaning and percentage time of antennule retraction, Figs. 5–6, a, b) and appear to be actively sensing the environment. In contrast, the strategy of the weak regulator (*Cancer magister*) and the osmoconformer (*Libinia emarginata*), after a short escape attempt, was to become quiescent and essentially isolate the main osmoregulatory organs, the gills, by decreasing passage of water through the branchial chambers. In addition to this isolation response, the chemoreception ability appears to have been compromised by the reduction in salinity, and the crabs no longer sampled the water by active movement of the antennules (Fig. 6c, d). Since most salinity variation is linked to the daily tidal changes, short-term isolation mechanisms may help reduce energy expenditure associated with escape responses or active regulation of the body fluids.

Many of the behaviors documented in the present study can be directly correlated with changes in the cardiovascular and osmoregulatory physiology. Previous reports on the inherent variability and discrepancies between studies of crustacean cardiovascular dynamics (Spaargaren, 1974; Hume and Berlind, 1976; Cumberlidge and Uglow, 1977; Taylor *et al.*, 1977; McGaw *et al.*, 1994b) are paralleled by intraspecific differences in behavior; as reported in the present study, a percentage of animals of each species exhibit a specific behavior, but some individuals may not. The causes of these discrepancies are unclear, but could be subtle differences such as intermolt duration or hormonal state, which can affect physiological ability (Reid *et al.*, 1989; McGaw and Naylor, 1992a, c; McGaw *et al.*, 1994b). The present study underscores the importance of studying behavioral reactions in conjunction with physiological measurements. Moreover, it provides evidence that well-studied gross physiological mechanisms to compensate for disturbances are linked with more subtle, behaviorally related modulations.

Acknowledgments

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